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ECOLOGY OF SMALL MAMMALS ON TWO ISOLATED BUTTES IN CANYONLANDS NATIONAL PARK, UTAH

DAVID W. JOHNSON

ABSTRACT.—Fewer mammalian species occurred on summits of sheer-walled buttes than occurred in similar “mainland” control sites, but density of small mammals on buttes equaled or exceeded mainland density. *Peromyscus crinitus*, the only terrestrial mammal on Jug Butte, occupied a larger habitat niche there than in control areas. No such niche expansion was noted for *P. crinitus* on Junction Butte, where four other species of small mammals (*Eutamias quadrivittatus*, *Neotoma lepida*, *Neotoma cinerea*, *Peromyscus truei*) and at least one large mammal (*Canis latrans*) also occurred. At least 18 species of terrestrial mammals inhabit the control sites. It is hypothesized that the species number remains static on each butte and is a function of the unique dispersal abilities of each species and does not represent an equilibrium between recurrent colonization and extinction.

The Island in the Sky District of Canyonlands National Park is composed of a large central mesa (approximately 80 km²) with deep canyons radiating down to a surrounding bench called the White Rim. Deep canyons also cut into the White Rim and lead down 300 m to the Green River on the west and the Colorado River on the east. Erosion has gouged deeply into the Island in the Sky and has cut through some peninsulas of the mesa, forming free-standing isolated buttes such as The Jug and Junction Butte. Like islands, these buttes support habitats separated from areas of similar habitat on the mainland mesa by the 150-m high Wingate sandstone cliffs which form the buttes. Also like islands, movement by some taxa to and from these isolated habitats may be limited by the cliffs, resulting in exclusion of some species from the buttes' summits.

Little is known about the organisms inhabiting these areas. In 1937, Anthony scrambled up Shiva Temple in the Grand Canyon, and because access to the summit was easy, all small mammal species expected in that habitat were found. Mason and West (1970) flew to the summit of Timber Top Mesa, a sheer-walled mesa in Zion National Park, Utah, to study the ecology of naturally occurring fires, but only noted the presence of “small rodents, birds and insects.” In Canyonlands, the only previous research concerning isolated buttes was a survey of the vegetation of Junction Butte (Loope, 1977). Armstrong (1979a, 1979b) studied mammals of Canyonlands, but did not investigate butte faunas.

Since isolated buttes are similar to islands in certain respects, their mammalian faunas may exhibit several of the phenomena typical of islands. Insular faunas generally have a lower species richness than mainland faunas (Case, 1975; Crowell and Pimm, 1976; Lack, 1971; Vaughan and Schwartz, 1980), with larger islands supporting more species than smaller islands (Lowe, 1955; MacArthur and Wilson, 1967; Simberloff, 1976). MacArthur and Wilson (1967) state that the lower species diversity on islands results from the different migratory abilities of the mainland species and that the number of species on an island is an equilibrium between rates of recurrent

colonization and extinction. The magnitude of this equilibrium is related directly to the area of the island and inversely to the proximity of the island to the mainland source of colonizers.

Because island faunas generally lack some of the species which normally occupy similar habitats on mainlands, many island species exhibit expanded habitat, food, and spatial niche dimensions (Cameron, 1962; Diamond, 1970; Grant, 1965; Lack, 1971). Usually concomitant with expanded niches, islands support a greater number of individuals per species (Grant, 1965) and may have total densities per taxon equaling or exceeding mainland levels (Case, 1975). This density compensation has been recorded for island lizards (Bennett and Gorman, 1979; MacArthur, 1972), birds (Cruz, 1977; Grant, 1965; MacArthur et al., 1972), and mammals (Sullivan, 1977; Webb, 1965).

The faunas of many island-like habitats (so-called habitat islands) such as caves (Culver, 1970), lakes and springs (Barbour and Brown, 1974; Brown, 1971; Aho, 1978), rivers (Sepkowski and Rex, 1974), cushion plants (Tepe-dino and Stanton, 1976), eastern U.S. woodlots (Gottfried, 1979), California oak forests (Opler, 1974), British trees (Strong, 1974), badger mounds (Platt, 1975), Great Basin mountaintops (Brown, 1971, 1978) and Andean paramo habitats (Vuilleumier and Simberloff, 1980) have been examined in light of island biogeography theory. In general, these studies support a positive species-area relation, but often historical or ad hoc explanations are sufficient to account for the species present.

Since the isolated buttes on the Colorado Plateau were (and still are) virtually unstudied, the present study was undertaken to (1) determine which, if any, terrestrial mammals inhabit isolated buttes and (2) determine the applicability of island biogeography theory to the mammalian faunas of these buttes.

STUDY SITES.—Field work was conducted in Canyonlands National Park, Utah, from 25 September 1975 through 10 December 1975 on four study sites: two isolated buttes and two control areas on the Island in the Sky Mesa. Buttes were chosen on the basis of size, degree of isolation from the surrounding habitat, and habitat similarity. Controls were chosen because habitats were similar to those on buttes.

The Jug is an isolated butte located 0.4 km SW of the Island in the Sky Mesa in Holeman Spring Basin (Sec. 34, T27S, R18E, Upheaval Dome Quadrangle, Utah). It rises approximately 400 m from the White Rim to an elevation of 1,761 m. The final 130 m is sheer Wingate sandstone capped with Kayenta sandstone, except at the northeastern end of the butte, where a remnant of Navajo sandstone overlies the Kayenta. The summit of the butte is approximately 5 ha and is divided into two major habitats. The southwestern two-thirds is an open juniper (*Juniperus osteosperma*) woodland with large areas of slickrock. Soil, where present, is thin, poorly developed, and composed either of sand or gravel. The northeastern third of the butte is a shadscale (*Atriplex confertifolia*)-blackbrush (*Coleogyne ramosissima*) community covering the gravelly cone leading to the summit cap of Navajo sandstone. The soil is poorly developed, but deeper than that found on the southwestern part of the butte. Access to the Jug was by helicopter. To the best of my knowledge, the summit had not been visited by man prior to this study.

The first control site was located at the head of a canyon in the west-central portion of Red Sea Flat on the Island in the Sky Mesa at an elevation of 1,768 m (Sec. 9, T27S, R19E). Substrate, physiography, and vegetation are similar to those of the Jug, and like the Jug the site supports two vegetation types—open woodland and brushland. The western three-fifths of the site is an open pinyon (*Pinus edulis*)-juniper woodland with large areas of slickrock and thin, poorly developed, sandy soil. The underlying rock is Kayenta sandstone. The eastern two-fifths of the site is

TABLE 1.—Per cent canopy coverage of common plant species in each study area (x = species known to be present but not sampled, o = species known not to be present). Per cent coverage of the two dominant species at each site are italicized.

Species	Jug		Junction Butte	Red Sea Flat		Grandview Point
	Woodland	Brushland	Woodland	Woodland	Brushland	Woodland
<i>Juniperus osteosperma</i>	6.75		6.60	7.63	3.82*	8.22
<i>Pinus edulis</i>	o	o	o	6.76	3.33*	0.88
<i>Artemisia bigelovii</i>	2.95	x	2.75	x		x
<i>Atriplex confertifolia</i>	0.52	7.70				
<i>Cercocarpus intricatus</i>			x	0.63		0.23
<i>Cercocarpus montanus</i>	0.38		8.94	0.86		2.83
<i>Chrysothamnus</i> sp.	1.80		x	0.45		x
<i>Coleogyne ramosissima</i>	0.71	2.50	x	2.95	14.26	6.80
<i>Cowania mexicana</i>	1.10		x	0.38		x
<i>Echinocactus</i> sp.	x	0.30	x	x		x
<i>Ephedra viridis</i>	1.70	0.05	2.00	x	3.33	0.64
<i>Fraxinus anomala</i>				0.94		2.40
<i>Gutierrezia</i> sp.	0.20	0.30	x	x	0.29	x
<i>Mahonia fremontii</i>					x	
<i>Opuntia</i> sp.	x	0.05	x	x	1.52	x
<i>Rhus trilobata</i>	1.90		x	x		x
<i>Yucca harrimanniae</i>	1.20	x	x	x	x	x
<i>Aristida longiseta</i>					0.29	
<i>Aster bigelovii</i>		0.30	0.50	x		
<i>Bouteloua curtispindula</i>	x	x	x		x	
<i>Bouteloua gracilis</i>				x		
<i>Bromus tectorum</i>	x			x		x
<i>Chaenactis</i> sp.		0.90				
<i>Cryptantha</i> sp.	x					
<i>Festuca octoflora</i>	x	0.05			x	
<i>Hilaria jamesii</i>	0.23	4.30	x	x	0.15	x
<i>Oryzopsis hymenoides</i>	x	x	x	x	0.69	x
<i>Sporobolus airoides</i>					0.10	
<i>Sporobolus cryptandrus</i>		0.05				
<i>Stanleya pinnata</i>	x	x	x	x		x
<i>Stipa comata</i>			x		0.19	
Total canopy coverage	19.44	16.50	20.79	20.60	27.88	22.05
Total number of species	19	16	19	21	15	20

*occur mostly at the edge of the stand.

blackbrush. The sandy soil of this shrub area is fairly well developed and supports many plant species requiring deep eolian soils (Loope, 1977). A shallow arroyo cuts through the southern third of the site in an east-west direction.

Junction Butte is located 0.8 km S of the southernmost point of the Island in the Sky Mesa (Sec. 7, T29S, R19E). It rises approximately 445 m from the White Rim, with the final 137 m composed of sheer Wingate sandstone cliffs capped with Kayenta sandstone. The elevation of the study site is 1,926 m. Unlike the Jug, Junction Butte has a narrow break in its cliff face on the northwestern side, which allows the only relatively easy human access to the summit. Also unlike the Jug, the 35-ha summit of Junction Butte supports only one major habitat type, an open juniper woodland with scattered small stands of mountain mahogany (*Cercocarpus montanus*) and large areas of slickrock and thin gravelly or sandy soil.

The second mainland control site was approximately 1.8 km N of Junction Butte near the tip of Grandview Point on the Island in the Sky Mesa at an elevation of 1,829 m (Sec. 5, T29S, R19E). Like other study sites, it is an open pinyon-juniper woodland with large areas of slickrock and thin gravelly or sandy soil overlying Kayenta sandstone bedrock. A list of common plant species and their respective per cent canopy coverages (determined by the line intercept and Daubenmire canopy coverage methods) is presented in Table 1.

METHODS.—In three areas (Junction Butte and the controls), a 1-ha trapping grid was laid out with tape and compass. One hundred 8 by 9 by 23 cm folding aluminum Sherman live traps were placed at 10-m intervals. Because the Jug was wide enough to accommodate only six traps 10 m apart, one grid of 60 traps (60 m by 100 m) was placed in the woodland and a second adjoining grid of 40 traps (40 m by 100 m) was placed on the shadscale slope to form the 1-ha grid. Traps were baited with peanut butter and rolled oats at sunset and checked the following morning after sunrise. For a shorter period of time in each area, traps also were set during the day to sample the diurnal species. Trapping effort consisted of 1,312 trap-periods on the Jug, 800 on Junction Butte, 1,300 on Red Sea Flat, and 1,200 on Grandview Point, for a total of 4,612 trap-nights and trap-days.

For each individual caught, the following information was recorded: date, trap location, weight to the nearest 0.1 g (read from a Pesola spring scale), sex, age (juvenile, subadult, or adult based on pelage), reproductive condition, standard external measurements, and the substrate and plant species nearest the trap. Individuals were marked by toe clipping. If no plants were near the trap, a physical description of the trap's location (such as slickrock, rock overhang, gravel slope) was recorded. All of these microhabitat descriptors then were combined into 17 categories. Each capture was associated with only one descriptor. Animals were released at the place of capture. Trap-deaths were preserved as study skins and were deposited in The University of Wyoming Zoology Museum and at Canyonlands National Park, Utah.

Density estimates (and their variances) were calculated using the Manly-Parr technique (Manly and Parr, 1968; Seber, 1973). Because there were too few recaptures of marked individuals of *Peromyscus crinitus* (canyon mouse) in areas other than the Jug, the Lincoln Index was used to estimate canyon mouse densities in these areas (Overton, 1971). Relative densities of canyon mice (number of trap-nights per capture) were calculated for comparison with unpublished data gathered by D. M. Armstrong.

Niche breadth (B_i) was calculated by $B_i = -\sum p_{ij} \log_{10} p_{ij}$ (Shannon and Weaver, 1949) where p_{ij} = proportion of species i associated with microhabitat descriptor j , and niche overlap (C_{ih}) was calculated by $C_{ih} = 1 - \frac{1}{2} \sum |p_{ij} - p_{hj}|$ (Horn, 1966) where p_{ij} is the same as before and p_{hj} = proportion of a second species associated with microhabitat descriptor j . Values of C_{ih} vary between 0 and 1, with 1 indicating complete overlap. The comparisons of B_i within species between sites are of interest.

RESULTS.—Eleven mammalian species were trapped in a total of 570 captures in all four study areas (Table 2). Due to use of small Sherman live traps, mammals larger than woodrats were not sampled. I saw desert cottontails and coyotes, and deer tracks at both control sites, but found no evidence of cottontails or mule deer (*Odocoileus hemionus*) on Junction Butte, although I did see a coyote track. For descriptions of rodent species occurring in the Island in the Sky District see Armstrong (1979b).

TABLE 2.—Total number of mammal captures (number of individuals in parentheses) trapped at the four study sites in Canyonlands National Park.

Species	Jug Butte	Junction Butte	Red Sea Flat	Grandview Point
<i>Eutamias quadrivittatus</i>		46(11)	38(16)	1(1)
<i>Ammospermophilus leucurus</i>			3(3)	26(12)
<i>Perognathus apache</i>			6(2)	
<i>Dipodomys ordii</i>			6(3)	
<i>Peromyscus crinitus</i>	248(46)	15(7)	8(4)	1(1)
<i>Peromyscus maniculatus</i>			49(21)	15(5)
<i>Peromyscus boylii</i>				5(1)
<i>Peromyscus truei</i>		6(2)	40(12)	10(2)
<i>Onychomys leucogaster</i>			4(1)	
<i>Neotoma lepida</i>		12(5)	10(3)	14(3)
<i>Neotoma cinerea</i>		2(2)		5(1)
Total number of species	1	5	9	8

On the Jug, only one species, the canyon mouse (*Peromyscus crinitus*), was captured and apparently it was the only terrestrial mammal present. Junction Butte, by contrast, supported four nocturnal species and one diurnal species: canyon mouse, pinyon mouse (*Peromyscus truei*), desert woodrat (*Neotoma lepida*), bushy-tailed woodrat (*N. cinerea*), and Colorado chipmunk (*Eutamias quadrivittatus*). In addition, coyotes and possibly mountain lions visit the area via the break in the cliffs. All five of the rodent species were captured on at least one "mainland" site, but the following six other species were captured exclusively in the control areas: antelope ground squirrel (*Ammospermophilus leucurus*), deer mouse (*Peromyscus maniculatus*), Apache pocket mouse (*Perognathus apache*), Ord's kangaroo rat (*Dipodomys ordii*), northern grasshopper mouse (*Onychomys leucogaster*), and brush mouse (*P. boylii*). In addition to the species captured, at least 15 more terrestrial mammalian species probably occur in the control areas (Armstrong and Johnson, 1980). To summarize, the buttes support only one to five species, while similar control sites support at least twice as many.

The density of *P. crinitus* (the only mammal captured) on the Jug was 41/ha ($s^2 = 0$). On Junction Butte, the best density estimate (for all five species) was 19 small mammals/ha ($s^2 = 2.6$). The best estimate for total small mammal density (nine species) at the Red Sea Flat site was 35/ha ($s^2 = 16.8$), and 20/ha ($s^2 = 0.5$) for the eight species at Grandview Point.

Density of *P. crinitus* only in the other study areas was estimated with the Lincoln Index. Using this method the Jug had a density of *P. crinitus* of approximately 43/ha, Junction Butte supported 5-6/ha, Red Sea Flat 5-6/ha and Grandview Point only 1/ha. This density on Grandview Point results from only one capture of *P. crinitus* in 600 trap-nights. These estimates show a seven-fold difference in the densities of *P. crinitus* on the Jug and those inhabiting Junction Butte and Red Sea Flat. Further evidence of this dramatic difference is shown by the relative densities of *P. crinitus* in the four study sites and on the Island in the Sky Mesa as a whole (Armstrong, unpublished). One *P. crinitus* was captured every 4.2 trap-nights on the Jug. This figure decreased to one capture per 28.6 trap-nights on Junction Butte, one per 125 trap-nights at Red Sea Flat, and one per 600 trap-nights on Grandview Point. Armstrong (unpublished) caught one *P. crinitus* every 24.4 trap-nights on Island in the Sky Mesa.

Percentages of each mammalian species associated with each microhabitat descriptor in each study site were calculated. Again, each capture was associated with only one descriptor. Except for the deep sand substrate (which occurred only in the Red Sea Flat brushland), all descriptors occurred at all sites. Results are summarized by species in the following paragraphs.

On the Jug, *P. crinitus* was associated with 13 of the 14 possible descriptors. Nearly half the animals were caught on bare rock. All but 2% of captures associated with vegetation were on rocky substrate. In all, 94% of captures were associated with rocky substrate. At the remaining three sites, the canyon mouse was caught exclusively on a rocky substrate, whether vegetated or not. On Junction Butte and at Red Sea Flat, 40% of captures were associated with bare rock, whereas approximately 60% were associated with

trees and shrubs on slickrock. The only *P. crinitus* caught at Grandview Point was associated with a tree on slickrock.

While the pinyon mouse was associated with as many as seven descriptors (at Red Sea Flat), it was associated mostly with trees or shrubs or bare rock. At no site was this species caught far from a stand of pinyons or junipers.

Peromyscus maniculatus was caught only at Red Sea Flat and Grandview Point. At Red Sea Flat over 80% of captures were associated with shrubs or grasses and forbs on deep sandy soil; remaining captures were associated with bare rock and trees. At Grandview Point there is no deep sandy soil; 20% of captures were on bare rock, 60% were associated with trees and shrubs on rock, and 13% with shrubs on a thin sand substrate.

Peromyscus boylii was captured on Grandview Point with the following associations: slickrock and boulders, 33%; trees on slickrock, 50%; shrubs on gravelly soil, 17%.

On Junction Butte, 33% of desert woodrats were captured on bare rock, 8% were captured near trees on slickrock, and 58% were captured near shrubs on slickrock. Eighty per cent of the *N. lepida* caught in the Red Sea Flat area were associated with bare rock and 20% were associated with trees on slickrock. Only 7% of captures were associated with bare rock and shrubs on thin sand on Grandview Point, whereas nearly 86% were associated with trees and shrubs on a rocky substrate.

All of the individuals of *N. cinerea* on Junction Butte were caught in slickrock and boulder areas. On Grandview Point, however, 40% were associated with trees on slickrock, 40% with shrubs on slickrock, and 20% with shrubs on a gravel substrate.

Chipmunks on Junction Butte were caught mostly on bare or vegetated rocky substrate. Only 4% of captures were made on thin sandy soil. At Red Sea Flat, half of the captures were on bare slickrock, 37% were associated with trees and shrubs on slickrock, and 13% with trees and shrubs on sand. The only chipmunk captured on Grandview Point was caught on bare slickrock.

All antelope ground squirrels captured at Red Sea Flat were associated with shrubs on deep sandy soil. On Grandview Point, where no deep sand deposits exist, 43% were captured in shrub areas on a gravel substrate, 21% were associated with trees on slickrock, 22% were associated with bare rock substrate, and 4% each were associated with an unvegetated gravel flat, shrubs on slickrock, or shrubs on shallow sand.

Both *Onychomys leucogaster* and *Dipodomys ordii* were captured exclusively in the shrub area with deep sandy soil at the Red Sea Flat site. *Perognathus apache* was caught only at the Red Sea Flat site, with 83% associated with shrubs in deep sandy soil, and 17% with grasses and forbs in deep sand.

Habitat niche breadth for each small mammal species was calculated for each study site (Table 3). *P. crinitus* on the Jug had the broadest niche of any of the species captured (0.90), although in areas other than the Jug the canyon mouse had approximately the same niche breadth as the other nocturnal woodland species. The species with the narrowest niches were primarily those inhabiting only the sandy brushland at Red Sea Flat: *O. leucogaster*, *D. ordii*, and *P. apache*. Although *N. cinerea* also occupied a narrow

niche on Junction Butte, the measure probably reflects the limited number of captures made of this woodrat.

Tables 4 and 5 present microhabitat overlap values for the mammal species at sites other than the Jug. On Junction Butte, *P. crinitus*, *P. truei*, *N. lepida*, and *E. quadrivittatus* displayed considerable overlap in habitat preference. Only the two woodrat species lack a high degree of overlap, but this low overlap again may reflect the dearth of bushy-tailed woodrat captures. Average niche overlap among all species captured more than twice was 0.44.

There are two major patterns of niche overlap at the Red Sea Flat site. *P. crinitus*, *P. truei*, and *E. quadrivittatus* exhibited little niche overlap with *A. leucurus*, *D. ordii*, *O. leucogaster*, and *P. apache*, but the last four species displayed high overlap among themselves and with *P. maniculatus*. The average overlap among all the species at the site was 0.36, but the overlap of the five species caught in the woodland was 0.37.

There was moderate overlap between the species at Grandview Point, with the highest degree of niche overlap displayed by the two woodrat species (0.84). Average overlap among the species was 0.56, greater than that at either Junction Butte or Red Sea Flat.

DISCUSSION.—Mammalian faunas of buttes had fewer species than mainland faunas, but total densities of small mammals on the buttes nearly equaled or exceeded the mainland levels. MacArthur et al. (1972) suggested that excess density compensation may be due to several ecological differences between an island and the mainland. These differences probably apply to the present study in the following ways. First, large species tend to be under-represented on islands, probably because they are not able to cross barriers and reach islands as easily or as often as smaller species. This is the case on the Jug; *P. crinitus* is a small-sized *Peromyscus* and is the only terrestrial mammal on the butte. Second, predation intensity may be lower on islands. While many reptilian, avian, and mammalian predators inhabit Island in the Sky Mesa, the only two potential predators that could affect canyon mice on the Jug are owls and snakes; I observed neither during my 12-day stay on the butte. Third, a wider range of resources is available per species on islands because there are fewer species present. In habitat similar to the Jug, the mainland supports at least four other species of small mammals and several species of larger mammals. Although mammals on Junction Butte did exhibit some density compensation, it was not to the degree shown by the Jug population.

Concomitant with increased density on the Jug, the canyon mouse increased its range of microhabitat use and was associated with 13 of the 14 possible microhabitat descriptors. At the other sites it had a niche breadth similar to those of other *Peromyscus* species.

Where the canyon mouse inhabited an area with other *Peromyscus* species, it had a low density; in areas without congeners, it had a high density. Some competitive mechanism may be regulating the density of *P. crinitus*. Hall (1946) found that *P. eremicus*, *P. truei*, and *P. maniculatus* can invade and inhabit *P. crinitus* habitat when *P. crinitus* is present. This finding suggests that *P. crinitus* cannot compete very successfully with these other

species and responds by decreasing its population size and area of activity, but the exact mechanism of competition is unknown. Since *Peromyscus* is omnivorous, competition for food may be low. If competition for food does not limit population size, perhaps behavioral factors are responsible.

Bradshaw (1965) found that *P. leucopus* and *P. gossypinus* segregate their mutual areas partly by habitat preference and partly by differential aggressiveness. King (1957) found that the more aggressive *Mus* could drive *Peromyscus* out of its natural habitats. This aggression often was manifested by direct physical attacks on *Peromyscus*. Differing levels of aggressiveness coupled with specific habitat preferences may allow the four species considered in the present study to coexist, albeit at densities lower than if they were alone. The canyon mouse may be the least aggressive of the four species and is forced to contract its range of shared habitats. Where it does not have to compete with other species, as on the Jug, it expands its niche spatially.

Why is there only one species of small mammal on the Jug, but five species on Junction Butte, and at least eight species on the mainland mesa? Several possible factors could account for these observations. For a species to colonize a butte successfully, it must be exposed to the opportunity to disperse to the butte, be able to climb to the summit, and find suitable, unoccupied habitat on the summit.

Several species are not found near the buttes. Kangaroo rats, pocket mice, and grasshopper mice require deep sandy soil and open vegetation (Armstrong, 1979a), habitat rare around the bases of these buttes. Although chipmunks, woodrats, and antelope ground squirrels inhabit the rocky open woodland near the buttes, only chipmunks and woodrats find the habitat in the break in Junction Butte's cliffs suitable. The sheer, virtually barren cliffs of the Jug are suitable for none of the three. Even though appropriate habitat for these species is present on the summit of the Jug, the sheer, virtually barren cliffs present impassable physical and ecological barriers. Halfpenny et al. (1977) found deer mice, bushy-tailed woodrats, and chipmunks on the summit of Devil's Tower in Wyoming. However, the volcanic cliffs forming

TABLE 3.—Niche breadth of each small mammal species captured at the four study sites. JB = Junction Butte, RSF = Red Sea Flat, GP = Grandview Point.

Species	Jug	JB	RSF	GP
<i>P. crinitus</i>	.90	.37	.57	0*
<i>P. truei</i>		.38	.68	.51
<i>P. maniculatus</i>			.44	.70
<i>P. boylii</i>				.44
<i>N. lepida</i>		.44	.41	.62
<i>N. cinerea</i>		0**		.46
<i>E. quadrivittatus</i>		.58	.50	0*
<i>A. leucurus</i>			0	.62
<i>O. leucogaster</i>			0	
<i>D. ordii</i>			0	
<i>P. apache</i>			.18	

*Only one capture; **only two captures.

TABLE 4.—Niche overlap between the small mammals on Junction Butte (above 'X' diagonal line) and between the small mammals on Grandview Point (below 'X' diagonal line). *Pc* = *Peromyscus crinitus*, *Pm* = *Peromyscus maniculatus*, *Pt* = *Peromyscus truei*, *Pb* = *Peromyscus boylii*, *Nl* = *Neotoma lepida*, *Nc* = *Neotoma cinerea*, *Al* = *Ammospermophilus leucurus*, *Eq* = *Eutamias quadrivittatus*. Values vary from 0 to 1, with 1 indicating complete overlap. (Blank indicates species pair not occurring at that site.)

	Pm	Pt	Pb	Nl	Nc	Al	Eq
Pc		.60		.82	.33		.76
Pm	×						
Pt	.53	×		.67	0		.58
Pb	.43	.57	×				
Nl	.78	.49	.53	×	.17		.68
Nc	.63	.60	.57	.84	×		.33
Al	.47	.46	.60	.52	.46	×	
Eq							×

the Tower are structurally more complex than those of the Jug and may provide more microrelief, allowing more species to ascend to the summit.

The canyon mouse inhabits rocky areas (see Armstrong, 1979a; Honeycutt et al., in press). Canyon mouse habitat is sharply restricted to rocky substrates—cliffs, boulders, talus slopes—where nests are built in crevices and under rocks. Mice are absent from areas lacking rocks. Vegetation per se has little or no effect on this species' distribution (Egoscue, 1964). Abbott (1971) and MacMillen (1972) found that *P. crinitus* is not dependent on free water or moist vegetation for survival. Like some other desert mammals, the canyon mouse conserves water by producing a concentrated urine and gains water by eating many insects. A further adaptation to its xeric, rocky habitat is its "keen ability to walk down and run up vertical rock surfaces" (Ryan, 1968:97). The long tail and long hind feet (as compared to some other species of *Peromyscus*) aid *P. crinitus* in climbing. Therefore, of the four *Peromyscus* species in the area, *P. crinitus* is one species that one would expect to find atop the least accessible buttes. Its predilection for rocky cliff habitats, regardless of vegetation types, has been established. It is an excellent climber, is not dependent on free water or moist plants, and is often caught on unprotected, exposed slickrock.

Peromyscus truei is associated closely with pinyon-juniper woodland. Pinyon mice may venture out of the woodland to feed, but are usually not residents of other habitats (Douglas, 1969).

TABLE 5.—Niche overlap in the small mammals at Red Sea Flat. Abbreviations and value range as in Table 4, plus *OI* = *Onychomys leucogaster*, *Do* = *Dipodomys ordii*, *Pa* = *Perognathus apache*. For convenience, high and low niche overlap values are boldfaced.

	Pt	Pm	Nl	Eq	Al	Do	OI	Pa
Pc	.46	.15	.53	.53	0	0	0	0
Pt		.27	.38	.59	.10	.10	.10	.08
Pm			.15	.20	.68	.68	.68	.81
Nl				.40	.52	0	0	0
Eq					.03	.03	.03	0
Al						1.00	1.00	.86
Do							1.00	.86
OI								.86

The pinyon mouse has a long tail and long hind feet relative to its body length, characteristic of semiarboreal forms of *Peromyscus* (Horner, 1954). If woodland is present on the route to a butte summit, *P. truei* should reasonably be there also. This is the case on Junction Butte. There is woodland at the base of the butte, scattered trees up the break in the cliffs, and woodland on the summit.

Peromyscus boylii is restricted to dense brush (Armstrong, 1979a; Durrant and Dean, 1959). A combination of lack of dense brush and the presence of two or three other *Peromyscus* species may be excluding *P. boylii* from the sites. Additionally, neither the cliffs of the Jug nor the break in the cliffs of Junction Butte provides suitable habitat for the brush mouse.

Peromyscus maniculatus is one of the most ubiquitous mammals in North America. It occurs in nearly every terrestrial habitat in Utah (Durrant, 1952). In Canyonlands National Park it is primarily a grassland species, although it is not restricted to that type. It also occurs in disturbed woodland and brushland areas. *P. maniculatus* often invades disturbed or ephemeral habitats. Grandview Point is a disturbed habitat with a graded road and numerous tourists. Grassland deer mice such as those in the present study generally are short-tailed, short-footed forms, and are not proficient climbers (Horner, 1954) and therefore may find the cliffs of the Jug unsuitable habitat. The route to the summit of Junction Butte presents no insurmountable physical barrier to the deer mouse, but neither the break in the cliffs nor the summit has suitable unoccupied habitat and therefore the ecological barrier may be insurmountable.

On the basis of the data presented, I suggest that the primary factors regulating species richness on the buttes is the ability of each species to cross the cliff barriers and find suitable habitat on the summit. The cliff habitat filters out those species not adapted to cope with conditions on the barrier. Only those species which find suitable habitat both across the barrier and on the butte's summit compose the butte's fauna.

The number of species on the buttes may not be at an equilibrium between recurrent colonization and extinction. MacArthur and Wilson's theory of island biogeography (1967) stated that species composition changes as new species colonize an island and some species already on the island become extinct, resulting in little change in species number, but a turnover in species composition. In the case of isolated buttes, it is possible that neither species composition nor species number changes. The only species on the buttes are those able to cross the barrier. These species are not replaced by different colonizing species because no other species can cross the barrier to colonize the butte. This is markedly different from oceanic islands where many species are able to cross the water barrier and possibly colonize the island.

Brown (1971) stated that mammalian faunas of isolated mountain ranges in the Great Basin do not represent equilibria between rates of recurrent colonization and extinction, but are relicts of groups of species that colonized the mountains during the Pleistocene. At that time the barriers that currently isolate the peaks did not exist. At the present time there is no coloni-

zation of these mountains by highland species, only extinction of species already present.

Barbour and Brown (1974) distinguished four patterns of insular species diversity: 1) many island biotas represent equilibria between colonization and extinction; 2) some insular biotas represent equilibria between speciation and extinction, and may occur when habitat bridges admitted relatively few colonists sufficiently long ago for speciation to reach an equilibrium with extinction; 3) islands have less than equilibrium species numbers when few colonizers crossed a habitat bridge too recently for speciation to occur; and 4) islands have more than equilibrium species numbers when many colonizing species crossed a habitat bridge too recently for extinction to lower the numbers of species.

In the present study, butte faunas do not fit any of these patterns, but rather a fifth pattern: continual colonization of the "island," but only by certain species. Whereas many species can reach oceanic and land-bridge islands, only a certain limited number of species can reach a summit of a butte and the number of species inhabiting the butte is static.

By knowing the type of barrier the butte presents and the type of habitat on the summit, it should be possible to predict which species inhabit specific buttes. I would expect sheer-walled buttes (such as the Jug) to support only *P. crinitus*. As the steepness of the cliffs decreases, *E. quadrivittatus* and possibly *N. cinerea* would be found. With a distinct break in the cliffs (as on Junction Butte) more species would be able to cross the barrier according to the habitat of the break. With dense brush in the gap, *P. boylii* might reach the summit, and if additionally the soil is friable, *A. leucurus* might cross the barrier. With pinyons and/or junipers in the gap, *P. truei* probably would invade. In either case, assuming a rocky substrate, *N. lepida*, *N. cinerea*, and *E. quadrivittatus* would reach the summit. If the route to the summit were disturbed in some way (rock slide, fire, human disturbance), *P. maniculatus* might reach the summit. Only when the access route and the butte's summit have open vegetation on a deep sandy substrate, would *D. ordii*, *P. apache*, and *O. leucogaster* possibly be present.

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